COPROLITES CONTAINING PLANT MATERIAL FROM THE CARBONIFEROUS OF BRITAIN

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ABSTRACT. Coprolites containing plant material are described from the Middle Coal Measures (Westphalian B) of Swillington, near Leeds, West Yorkshire. Other possible coprolites from the Lower Carboniferous (Calciferous Sandstone Series) of the Loch Humphrey Burn and Glenarbuck localities in the Kilpatrick Hills, Strathclyde are also recorded. The Coal Measure specimens contain either lycopod megaspore fragments, indeterminate plant debris, or a large variety of microspores (attributable to Lycopsida, Sphenopsida, Pteropsida; Filicinae, Gymnospermae, and Pteridospermae) whereas the Lower Carboniferous specimens consist mainly of rolled plant debris. It is suggested that these coprolites belonged to animal litter feeders and is direct evidence of animals eating vegetation in the Palaeozoic.

AFTER a recent symposium on animal/plant interrelationships in the Palaeozoic, Cox (1974) concluded that 'there seems little chance of a great variety of unequivocal evidence for the interaction between Palaeozoic plants and arthropods'. Although recent studies have shown that some interrelationships between animals and plants may have existed as early as the Devonian (Kevan *et al.* 1975), it remains true that very little direct evidence of animals feeding on plants has been brought forward.

Leaves of *Neuropteris* with holes, presumably made by an herbivorous animal, have been reported from Coal Measure sediments (Van Amerom 1966; Van Amerom and Boersma 1971) and similarly eaten leaves of *Glossopteris* have been described from the Karroo rocks of South Africa (Plumstead 1963). Borings, possibly made by insects, have been reported in *Trigonocarpus* seeds from the Carboniferous (Barnard, oral comm., see Cox 1974). Animal damage of plant axes (Kevan *et al.* 1975) and trigonotarbid arachnids within sporangia have been described from the Devonian Rhynie Chert (Rolfe in Kevan *et al.* 1975, pl. 56). Numerous examples of damaged stems have been reported from the Carboniferous (*Calamites*, Seward 1898, Stopes 1907; *Myeloxylon*, Holden 1910; lepidodendroid axis, Wilkinson 1930) but it is uncertain whether these wounds were caused by natural accidents or whether they were the result of animal damage. A few specimens of bored Carboniferous wood have been figured (i.e. *Sigillaria*, Geinitz 1855, pl. 8, fig. 1) and in one specimen borings have been shown to contain minute ($< 100\ \mu m$) coprolites attributed to arthropods (Williamson 1880, pl. 20, figs. 65, 66). Other occurrences of damaged wood have been reviewed by Moodie (1923, pp. 99–108).

Unfortunately the morphology of Palaeozoic animals has not been of great help in the search for possible herbivores. The large Carboniferous 'centipede' *Arthropleura*, for example, was regarded as carnivorous on the basis of the nature of a supposed cephalic limb, but proved to have plant debris (?lycopod) in its gut (Rolfe and Ingham 1967).

The record of coprolites containing plant material has been very scanty. The contents of most coprolites are generally unidentifiable (phosphatized) or else they

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contain animal remains and are generally attributed to fish (see occasional references in Häntzschel *et al.* 1968). Coprolites from coal balls have been figured by Mamay and Yochelson (1962) and those consist of partly macerated plant material, mostly epidermal (Mamay, pers. comm. 1976). Brief mention is made of coprolites containing plant material by Cox (1974) but no details are given.

Other coprolites containing spores and pollen have been reported from post-Palaeozoic rocks. Harris (1957) described, from the Jurassic of Yorkshire, small coprolites containing *Caytonia* pollen and leaf cuticle of both *Sagenopteris* and *Gingko*. Bryant and Williams-Dean (1975) described subfossil human coprolites which contained plant material and pollen which have given information on both early human diet and local vegetation.

The occurrence of coprolites containing plant remains from the Coal Measures of Yorkshire and the Calciferous Sandstone of the Kilpatrick Hills is further direct evidence that some animals were exploiting this food source in the Carboniferous. The predominance of plant material in the coprolites strongly suggests that they were produced by herbivores and are not the undigested waste products of plants accidentally eaten by carnivores.

DESCRIPTIONS

Coal Measures

Twelve small coprolites were found in residues obtained by disaggregating shales in hydrofluoric acid. The shales (flood plain deposits) were thin partings in poor coal one metre below and immediately above the Lodgett Coal, Swillington Brickworks, near Leeds, West Yorkshire (SE 384314, Godwin and Calver 1975). These residues also contained abundant megaspores, cuticles, and fusain including an early conifer (Scott 1974).

The coprolites are generally cylindrical in shape (up to 3×1 mm), although some have been flattened. They are of three main types: one containing mainly lycopod megaspore fragments, one containing a mixture of microspores, and one containing indeterminate plant debris. The megaspore fragments may be identified from the nature of their sculptural elements. One coprolite (Pl. 13, figs. 1, 2) contained only fragments of the sigillarian megaspore *Tuberculatisporites mammilarius* (Bartlett) (Pl. 13, figs. 7, 11) whereas another (Pl. 13, figs. 3, 9, 14) contained mainly fragments of lepidodendroid megaspores such as *Lagenicula subpilosa* (Ibrahim) (Pl. 13, figs. 8, 12). Occasional *Lycospora*, other unidentifiable microspores, and cuticle are also found.

Those coprolites containing microspores are more irregular in shape, often considerably flattened probably because of the greater compressibility of the more finely divided plant material. This type of coprolite has a wide range of composition, some containing an abundance of two types of spore (Table 1, specimens 10 and 12) and others a large number of types (Table 1, specimens 6 and 8, Pl. 13, figs. 5 and 6, Pl. 14, figs. 1–9). (Numerous sporangia are found in the same residues but are recognized by containing only a single species of spore, layering, and by the undamaged nature of the spores, Pl. 13, figs. 4, 10.) Many of the microspores are exceptionally well preserved although many are also broken. The spores which are

TABLE 1. The Composition of Coprolites from the Westphalian B of Yorkshire. The specimens have been lodged in the Hunterian Museum, Glasgow (FSC 2061–2072).

Specimen no.	1	2	3	4	5	6	7	8	9	10	11	12
LYCOPSIDA—MEGASPORES												
Tuberculatisporites mammilarius (Bartlett)	A											
Lagenicula subpilosa (Ibrahim)							C					
Indeterminate			C				A	R				
LYCOPSIDA—MICROSPORES												
Lycospora (Schopf, Wilson and Bentall)		R				O	O	R				A
Densosporites (Berry)								O				C
cf. *Crassispora* (Bharadwaj)	R							?R				
?*Cristatisporites* (Potonié and Kremp)			O			O						
SPHENOPSIDA—MICROSPORES												
Calamospora Schopf, Wilson and Bentall						?A		?O				
?*Laevigatosporites* Ibrahim										A		
PTEROPSIDA—MICROSPORES												
FILICINAE												
cf. *Cyclogranisporites* Potonié and Kremp								?R				
Raistrickia (Schopf, Wilson and Bentall)								O				
cf. *Verrucosisporites* (Ibrahim)			A									
cf. *Savitrisporites* Bharadwaj								R				
GYMNOSPERMAE												
?*Florinites* Schopf, Wilson and Bentall				A								
PTERIDOSPERMAE												
Schopfipollenites Potonié and Kremp								R				
UNKNOWN AFFINITY												
cf. *Ahrensisporites* Potonié and Kremp								C				
cf. *Pustulatisporites* Potonié and Kremp						C		?C				
Indeterminate					O	O		C				
OTHER PLANT MATERIAL												
Indeterminate cuticle				?A	O	R	O	O	?A			
Indeterminate wood			C			O						
Indeterminate plant material		A	C		A	O	O	O	A	R	A	

R = Rare, O = Occasional, C = Common, A = Abundant.

recorded represent both a wide variety of morphologies and a number of diverse plant groups including lycopods (*Lycospora* and *Densosporites*, Pl. 13, fig. 5), ferns (*Raistrickia*, Pl. 14, fig. 8), pteridosperms (*Schopfipollenites*, Pl. 14, fig. 7), and sphenopsids (*Calamospora*) (Potonié 1962, 1965; Potonié and Kremp 1954).

It is concluded that these pellets are genuine coprolites, and not burrow fills, peat pellets, or sporangia, because of the repetition of constant shape and the heterogeneity of plant material. From the variety of plant material in the coprolites it appears that the animals concerned were more likely to have been litter feeders rather than direct cone or leaf feeders. There is no conclusive evidence that these coprolites all belong to the same type of animal, but from the general size and shape this seems a strong possibility.

There are a number of different kinds of animal, mainly arthropod, which may have been eating the plant litter and produced these coprolites. Although cuticle of arachnid type (Pl. 14, fig. 14, L. J. Wills and I. Strachan, pers. comm. 1975) has been found in this deposit there is no evidence to suggest that this was the animal responsible.

Lower Carboniferous, Calciferous Sandstone Series

(i) Loch Humphrey Burn

This material, from the Walton Collection in the Hunterian Museum, Glasgow (prefix Pb to numbers) comes from the Loch Humphrey Burn plant bed (Smith 1964) and is preserved as compression fossils. These 'coprolites' (Pl. 14, fig. 13) are fairly common and range in length from 20 to 26 mm (e.g. Pb 3313, 3314a, b, 2507, 2516) and when found unsquashed are approximately 7 mm in diameter (Pl. 14, fig. 12, Pb 3314c). The flattened cylinders generally show four longitudinal ridges as seen on a cleaved bedding surface (Pl. 14, fig. 13). In cross-section they show twelve prominent ridges (Pl. 14, fig. 12). It is not fully understood how in the same bed most of these 'coprolites' are flattened whilst one remains unsquashed. There is no way to prove that the two types of fossils are related, short of cleaving open the unsquashed specimen to look at the longitudinal view, but from the nature of the shape, a cylinder with prominent ridges, it would seem likely that they are similar objects. It will need, therefore, further specimens before the nature of preservation is fully understood.

When macerated these cylinders yield unidentifiable plant debris. They are thought not to be either burrow fills or peat pellets because of their constant shape, but there remains the possibility that they may be some poorly preserved plant organ rather than a coprolite, although the latter is favoured. There are no data concerning the animals that might have produced these ?coprolites.

EXPLANATION OF PLATE 13

Westphalian B coprolites and associated plant fragments from shaly partings below and above the Lidgett Coal, Swillington, West Yorkshire. All pictures were taken with a Cambridge S600 Scanning Electron Microscope (S.E.M.), the specimens having been coated with gold in a Polaron Sputter-Coating Unit E5000.

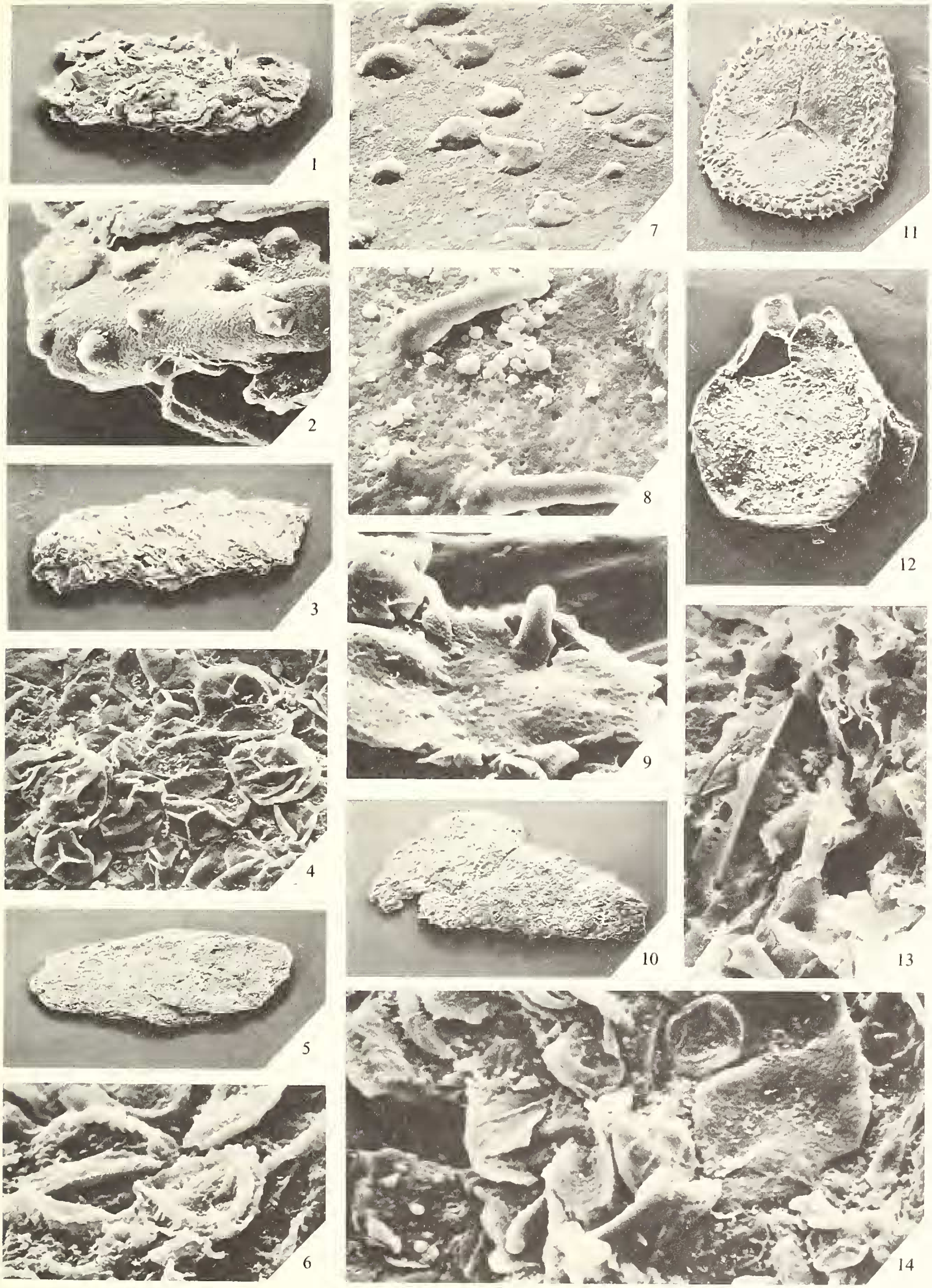
Figs. 1–3, 9, 14. Coprolites containing megaspore fragments. 1, whole coprolite, Table 1, specimen 1, ×40 (FSC 2061). 2, fragment of megaspore *Tuberculatisporites mammilarius* (Bartlett) from the same specimen, ×150 (FSC 2061). 3, whole coprolite, Table 1, specimen 7, ×40 (FSC 2067). 9, detail of megaspore fragment of *Lagenicula subpilosa* (Ibrahim) from the same specimen, ×250 (FSC 2067). 14, megaspore fragments, microspores, and plant debris from the same specimen, ×250 (FSC 2067).

Figs. 4, 10. Dispersed sporangium from the same horizon. 4, detail of spores, *Calamospora* Schopf, Wilson and Bentall, ×160 (FSC 2073). 10, whole sporangium, ×15 (FSC 2073).

Figs. 5, 6, 13. Coprolites containing microspores and plant debris. 5, whole doprolite, Table 1, specimen 3, ×15 (FSC 2063). 6, detail of same specimen with ?*Cristatisporites* (Potonié and Kremp), ×600 (FSC 2063). 13, detail of coprolite, Table 1, specimen 9, with abundant plant debris, ×225 (FSC 2069).

Figs. 7, 8, 11, 12. Megaspores from the same horizon. 11, *Tuberculatisporites mammilarius*, ×20 (FSC 2076). 7, detail of distal face, ×150 (FSC 2074). 12, *Lagenicula subpilosa*, ×25 (FSC 2075). 8, detail of spines, ×275 (FSC 2075).

All specimens have been lodged in the Geology Collection of the Hunterian Museum, Glasgow.



SCOTT, plant debris in Carboniferous coprolites

(ii) Glenarbuck

Three slides, in the Walton Collection, Hunterian Museum, Glasgow (FSC 779-781), show cross-sections of what have been interpreted (on Walton's slide label) as coprolites. These have a circular, although slightly irregular cross-section (Pl. 14, fig. 10) with a diameter of 5 mm (FSC 781 has a diameter of 1 mm but this may be because only the tapered end of the coprolite was sectioned). The three slides are probably peels from the same specimen. The plant material inside the ?coprolite is layered (Pl. 14, fig. 11) consisting mainly of stelar and woody elements and other unidentifiable plant material. For these specimens, however, there is less evidence that these are coprolites; they may be simply pellets of petrified peat.

No animal remains have been found in association with these ?coprolites.

DISCUSSION

Which animals produced these coprolites and which Palaeozoic animals were herbivores is a matter of speculation. Numerous types of insects were present in the Coal Measures, some of which may have been herbivores (phytophagous). It has been suggested that other arthropod groups such as the Collembola and Arachnida may have been litter feeders, as they are today (Tillyard 1931). The Collembola are also thought to have been spore feeders (Smart and Hughes 1973) as have some of the trigonotarbid arachnids already cited. Kevan *et al.* (1975) note that spores are often one of the alternative food sources 'adopted' by carnivorous (zoophagous) arthropods if animal food is lacking.

Of the insects, especially ground-dwelling species, cockroaches (Dictyoptera) were present in the Carboniferous (Müller 1963). I have examined the faecal pellets from an extant genus of the phytophagous cockroach, *Blaberus*, which is 6–7 cm

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EXPLANATION OF PLATE 14

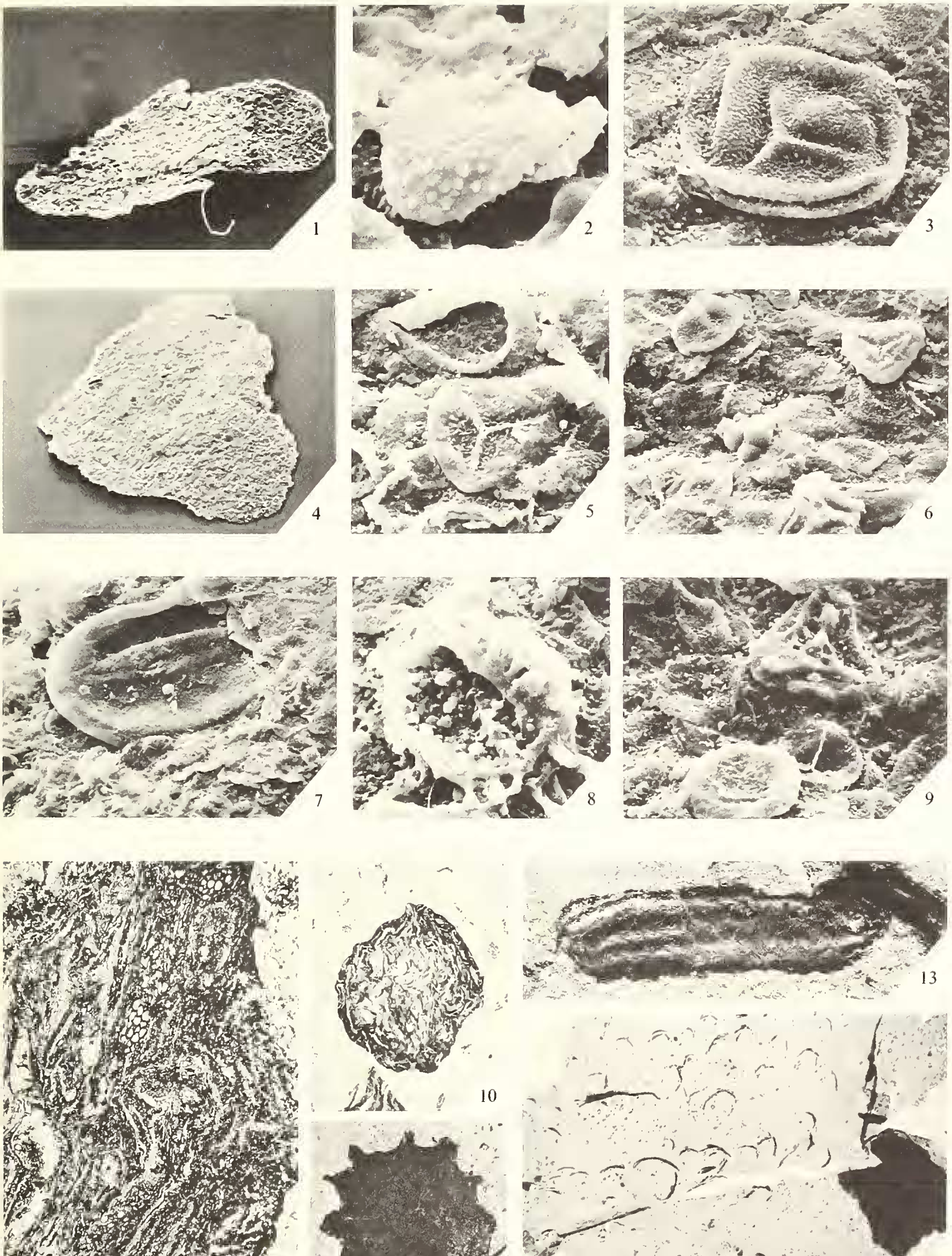
Figs. 1–9. Westphalian B coprolites from shaly partings below and above the Lidgett Coal, Swillington, West Yorkshire. (S.E.M. as Pl. 13.) These specimens (including fig. 14) have been lodged in the Geology Collection of the Hunterian Museum, Glasgow. 1, whole coprolite, Table 1, specimen 6, ×25 (FSC 2066). 2, detail of same specimen with a triangular microspore with conate ornament, ?*Pustulatisporites* Potonié and Kremp, ×600 (FSC 2066). 4, whole coprolite, Table 1, specimen 8, ×15 (FSC 2068). 3, detail of the same specimen with ?*Cyclogranisporites* Potonié and Kremp, ×450 (FSC 2068). 5, detail of the same specimen with *Lycospora* (Schopf, Wilson and Bentall) and ?*Denosporites* (Berry), ×600 (FSC 2068). 6, detail of the same specimen with numerous microspores including ?*Savitrisporites* Bharadwaj and ?*Ahrensisporites* Potonié and Kremp, ×300 (FSC 2068). 7, detail of the same specimen with *Schopfipollenites* Potonié and Kremp, ×250 (FSC 2068). 8, detail of the same specimen with *Raistrickia* (Schopf, Wilson and Bentall), ×600 (FSC 2068). 9, detail of the same specimen with microspores including ?*Ahrensisporites* Potonié and Kremp, ×500 (FSC 2068).

Specimens shown in figs. 10–13 are from the Walton Collection in the Hunterian Museum, Glasgow.

Figs. 10, 11. Cross-sections of ?coprolites from the Calciferous Sandstone Series of Glenarbuck. 10, whole cross-section, ×4 (FSC 780). 11, detail showing plant debris and stelar fragments, ×30 (FSC 780).

Figs. 12, 13. ?Coprolites from the Calciferous Sandstone Series, Loch Humphrey Burn. 12, cross-section, ×4 (Pb 3314c). 13, longitudinal cleavage compression, ×2 (Pb 2576).

Fig. 14. Animal cuticle (?Arachnid) from the shales below the Lidgett Coal, Swillington, West Yorkshire, ×8 (A 2618).



SCOTT, plant debris in Carboniferous caprolites long. These are small, 3 mm × 1 mm, roughly cylindrical, and occasionally show longitudinal striations. Smaller species would presumably produce smaller faecal pellets (perhaps comparable in size and shape to the Coal Measure specimens). Smart and Hughes (1973) suggest that the 'probosces of Palaeodictyoptera and Megasectoptera could have been used as a probe to work over cones and capsules of the plants of that time (Carboniferous) for spores and pollen and perhaps especially for megaspores . . .' which Kevan *et al.* (1975) observe must have represented a particularly nutritious food source for insects. The eating of spores by arthropods, it has been suggested, is likely to have contributed to spore dispersal and even when the spores have passed through the animals' gut some of them may still have remained viable (Chaloner 1976).

Other arthropods which are thought to have been phytophagous include the myriapods (Kevan *et al.* 1975; Rolfe and Ingham 1967). These include the millepedes which have Palaeozoic representatives (Hoffman 1969) and have been shown in some figures to be eating plant material including *Lepidodendron* (Hoffman 1969). I have examined the faecal pellets of an extant African millepede, 9 cm long. These consist of plant debris and measure 6 mm × 3 mm. The size of the faecal pellets, however, is not directly related to the length of the animal but to a combination of body weight and the quantity of food eaten at any one time (Edwards 1974). *Arthropleura*, a member of an extant group of myriapods, has been shown to be phytophagous. A juvenile specimen with lycopod fragments in its gut (Rolfe and Ingham 1967) might have produced faecal pellets about 4 mm in diameter (measured from Pl. 13, fig. 8). The adult animal which grew to 1·5 m long must have produced larger faecal pellets, perhaps the size of the Lower Carboniferous specimens, although the genus *Arthropleura* is only known from Upper Carboniferous deposits (Rolfe 1969).

Although most groups of extant arachnids are zoophagous some mites (Acarida) are phytophagous (Wallwork 1967). Most, however, are very small (less than 1 mm, Harding and Stuttard 1974). Some Palaeozoic forms are found up to 8 mm in length (Petrunkevitch 1955) and may have produced faecal pellets in the order of 1 mm long.

Few early vertebrates are thought to have been herbivores although the Upper Palaeozoic amphibian *Scincosaurus* which has spathulate teeth may be such an animal (A. Girvan, pers. comm.).

CONCLUSIONS

Considering the quantity of plant material available for exploitation as a food source, in the Carboniferous, it is surprising that previously very little direct evidence of herbivores has been found as ultimately all land fauna is dependent on land vegetation, forming the basis of an extensive food chain.

The occurrence of coprolites containing spores and plant tissue is direct evidence that at least some animals were exploiting this food source in the Carboniferous.

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